Increased stem density and competition may diminish the positive effects of warming at alpine treeline

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Yafeng Wang[1], Neil Pederson[2], Aaron M. Ellison[2*], Hannah L. Buckley[2,3], Bradley S. Case[2,4], Eryuan Liang[1,5*], J. Julio Camarero[6]

[1]*Key Laboratory of Alpine Ecology and Biodiversity, Key Laboratory of Tibetan Environment Changes and Land Surface Processes, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100085, China;*

[2]*Harvard Forest, Harvard University, 324 North Main St., Petersham, MA01366, USA;*

[3] *Department of Ecology, Lincoln University, Lincoln 7647, New Zealand;*

[4] *Department of Informatics and Enabling Technologies, Lincoln University, Lincoln 7647, New Zealand*

[5]*CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing 100101, China;*

[6]*Instituto Pirenaico de Ecología, CSIC (IPE-CSIC), Avenida Montañana, 1005, 50059 Zaragoza, Spain*

Corresponding authors:

Dr. Aaron M. Ellison, aellison@fas.harvard.edu

Dr. Eryuan Liang, liangey@itpcas.ac.cn

Abstract. The most widespread response to global warming among alpine treeline ecotones is not an upward shift, but an increase in tree density. However, the impact of increasing density on interactions among trees at treeline is not well understood. Here, we test if treeline densification induced by climatic warming leads to increasing intraspecific competition. We mapped and measured the size and age of Smith fir trees growing in two treelines located in the southeastern Tibetan Plateau. We used spatial point-pattern and codispersion analyses to describe the spatial association and covariation among seedlings, juveniles, and adults grouped in 30-year age classes from the 1860s to the present. Effects of competition on tree height and regeneration were inferred from bivariate mark-correlations. Since the 1950s, a rapid densification occurred at both sites in response to climatic warming. Competition between adults and juveniles or seedlings at small scales intensified as density increased. Encroachment negatively affected height growth and further reduced recruitment around mature trees. We infer that tree recruitment at the study treelines was more cold-limited prior to 1950 and shifted to a less temperature-constrained regime in response to climatic warming. Therefore, the ongoing densification and encroachment of alpine treelines could alter the way climate drives their transitions towards subalpine forests.

Key words: *climatic warming; codispersion; dendroecology; facilitation; long-term ecological process; paleoecology; plant interactions; point-pattern analysis; timberline.*

INTRODUCTION

Competition is a crucial driver of the structure, spatial patterns, and dynamics of forests (He and Duncan 2000, Comita et al. 2010). Tree-to-tree competition tends to increase with density of conspecifics (Kenkel 1988, Getzin et al. 2006). Therefore, densification and encroachment should intensify competition between trees even near the uppermost limit of their existence, the alpine treeline. Globally, an increase in forest density is being observed more frequently than altitudinal ascents of the uppermost trees at treeline (e.g., Camarero and Gutierréz 2004, Kullman 2007, Liang et al. 2011), and recent studies have discussed the potential for competition to shape recent treeline dynamics (Grau et al. 2012). However, little is known about the role of competition on long-term population dynamics of trees, as climatic warming usually ameliorates environmental conditions at treeline (Camarero and Gutiérrez 2004, Holtmeier and Broll 2007, Elliott 2011).

The highest alpine Northern Hemisphere treeline ecotones, such as those located across the Tibetan Plateau, experience extreme environmental conditions (Miehe et al. 2007) and thus provide an excellent system to investigate the impact of climatic warming on competition (Liang et al. 2011). Because low temperature often is the major constraint on tree regeneration, survival, and growth at alpine treelines (Wang et al. 2006, Holtmeier and Broll 2007, Liu and Yin 2013; Renard et al. 2016), recent treeline densification at treelines has been linked to rising temperatures (Liang et al. 2011, Lv and Zhang 2012). However, here we argue that rapid treeline densification would lead not only to increased positive spatial associations (i.e., clustered spatial patterns) among recruits (Batllori et al. 2009), but also to increased competition among adult trees and recruits. Competition in such early stages should be mainly asymmetrical, resulting from, and subsequently amplifying, different growth rates

among adjacent individuals (Fajardo and Mclntire 2007). Alternatively, if facilitation occurs among trees in the harsh conditions at treeline, positive spatial associations between tree height of adults and recruits would be observed. To test these ideas, we first reconstructed the age structure of Smith fir populations within two large plots spanning the upper boundary of treeline ecotones in the Tibetan Plateau and examined the relationship between age structure and recent climatic warming. We then analyzed the spatio-temporal treeline dynamics during the past 150 years by using spatial point-pattern and codispersion analyses. Finally, we inferred the possible impacts of recent densification on competition and treeline dynamics in response to climate.

METHODS

Study area

The study area is located in the Sygera Mountains in the southeastern Tibetan Plateau (29° 10’ - 30° 15’ N, 93° 12’ - 95° 35’ E) (Appendix S4: Fig. S1). The closest meteorological station, located in Nyingchi (Linzhi) (29° 34’ N, 94°28’ E, 3000 m a.s.l.), recorded 671 mm mean total annual precipitation (1960−2012 period), > 70% of which falls between June and September. A significant warming trend in summer (June to August) and winter (December to February) without a concomitant trend in annual or summer precipitation was detected there beginning in the 1960s (Liang et al. 2011). Another nearby automated meteorological station located at treeline in the Sygera Mountains (29° 40’ N, 94°43’ E, 4390 m a.s.l.) recorded a range in mean annual temperatures from -0.2 to 0.9 ^{o}C between 2007 and 2013 (Liang et al. 2011). July was the warmest month (mean temperature 7.9 ± 0.5 °C) and January was the coldest (mean temperature -8.0 ± 1.7 °C). This treeline station recorded an annual average of

957 mm of precipitation; 62% during the monsoon season (June -September), and snowfall occurred mainly from November - May.

Tree species

Smith fir (*Abies georgei* var. *smithii* (Viguie & Gaussen) W. C. Cheng & L. K. Fu) is the dominant tree species on the north-facing slopes in the Sygera Mountains, where it forms nearly monospecific stands between 3,300 m and 4,400 m a.s.l. The maximum elevation for Smith fir treeline varies from 4,250 to 4,400 m a.s.l., depending on local topographical conditions. Diffuse treelines are common on gentle slopes. As wind speeds are generally low, flagged trees or shrubby individuals ("krummholz") are usually absent in these treelines (Liang et al. 2011). The oldest individual Smith fir near the timberline is around 400 years old (Liang et al. 2011). July mean minimum air temperature appears to be the primary constraint on the radial growth of adult Smith fir (Liang et al. 2011). Seeds can be dispersed upslope up to 40 m away from parent trees located at treeline (Shen et al. 2014).

Field sampling

We characterized the structure and reconstructed the dynamics of Smith fir at two treeline sites, designated as "N1" and "N2". Both sites were located on north-facing slopes, and encompassed the treeline ecotone, including the upper treeline (uppermost 2-m tall trees) and the forest limit (elevation at which tree cover ≥ 30%). The current altitudinal positions of N1 and N2 were 4388 and 4370 m a.s.l., with mean slopes of 10º and 15º, respectively. These treelines were not locally disturbed by yak (*Bos grunniens*) grazing or logging (Liang et al. 2011), and defoliation due to insect outbreaks or wild herbivores were not observed during field sampling. Above the current treeline, dense 2-3 m tall individual *Rhododendron* shrubs dominated the vegetation, but no stumps or remains of old dead trees were found there.

The age structure of the Smith fir trees (DBH > 5 cm) within two large rectangular plots (150 × 150-m; see Appendix S4: Fig. S2) was characterized following Liang et al. (2011) and Wang et al. (2012). Age was estimated from basal cores taken from the main stem of each tree and collected with an increment borer (see Appendix S1 for additional methodological details). We processed the core samples using standard dendrochronological techniques, including air drying, sanding with successively finer sandpapers, and visually cross-dating the cores under a stereomicroscope (Cook and Kairiukstis 1990). Mean series intercorrelation for plots N1 and N2 were 0.61 and 0.60, respectively, indicating reliable cross-dating. If the pith was not present in the core, a pith geometric locator was used to estimate the innermost distance missing up to the theoretical center of the stem (Wang et al. 2012). Ages of hollow trees were estimated using DBH-age regressions (N1: $r^2 = 0.88$, $P < 0.001$, n = 385; N2: $r^2 = 0.83$, $P < 0.001$, n = 406; see also Liang et al. 2011). In our collection, missed piths typically occurred only in trees >200-years old, so any errors in estimated ages using this method would have little effect on recruitment that occurred within the last 150 years. The germination age of young individuals (DBH < 5 cm and height < 1.3 m, age > 3 years) was estimated by counting the successive bud scars or internodes observed along their main stem (Camarero and Gutiérrez 2004). Since uncertainties related to age determination were always present, we binned tree ages by decades for analysis (Liang et al. 2011).

To identify temporal changes in the variation in spatial patterns of Smith fir in these two plots, we examined tree size distributions in five consecutive 30-yr intervals beginning with the 1862−1891 period and ending either with 1982−2011 (for N1) or 1982−2013 (N2). For each interval, individual Smith fir trees were grouped into three age classes: seedlings (age ≤ 30 years), juveniles (31 ≤ age ≤ 100 years), and adults (age ≥ 101 years). These age classes

produced groups similar to those found when grouping trees by their height or DBH. For instance, a tree aged 30 years was often approximately 50-cm tall, a threshold which is often used as a criterion to define the maximum height of seedlings growing in treeline ecotones (Camarero and Gutiérrez 2004). Likewise, trees between 101 and 150 years in age corresponded to heights > 6 m with DBH > 17.5 cm, which are categories usually employed to consider a tree as a mature, dominant, and reproductive individual (Camarero and Gutiérrez 2004, Wang et al. 2012). Given the lack of long-term forest survey data near treelines (Liang et al. 2011, Wang et al. 2012), grouping trees into age or stage classes provides a reliable method to investigate the variations of competition through time.

Point-pattern analyses

To describe how the spatial patterns of the treeline Smith fir population changed through time, we used point-pattern analyses (Wang et al. 2010, Wiegand and Moloney 2004, 2014) implemented in the Programita software (Wiegand and Moloney 2014). We used inhomogeneous versions of the univariate and bivariate $O(r)$ statistics because they are sensitive to variation in patterns at small spatial scales (Wiegand and Moloney 2004, 2014) and there is environmental heterogeneity within Smith fir treeline ecotones (Wang et al. 2012). The univariate $O_{11}(r)$ statistic was used to characterize the spatial patterns of the three different age classes, and the bivariate $O_{12}(r)$ statistic was used to characterize the spatial associations between the three age classes. Values of $O_{11}(r)$ located above or below the upper and lower envelopes represent significant aggregation or hyperdispersion (regularity), respectively, whereas values of $O_{12}(r)$ located above or below the upper and lower envelopes represent significant attraction or repulsion, respectively (see Appendix S2 for more additional technical details about the analyses).

Mark correlation function: bivariate patterns with a quantitative mark

We used the normalized mark correlation functions $k_{m1m2}(r)$ of tree heights to examine how patterns of growth covaried among age classes. This was justified because tree height was measured for all sampled individuals, and height growth is used to define treeline position (Holtmeier and Broll 2007). Further, competition among trees and its effects on growth are described better by considering heights of neighboring tree than by measuring their DBH (Thorpe et al. 2010). Bivariate point pattern analysis on a quantitative attribute (or "mark"), such as tree height, can be used to explore the impact of individuals of one pattern (e.g., bigger or older individuals) on individuals of a second pattern (e.g., smaller or younger individuals).

Using $k_{m1m2}(r)$ accounted not only for the spatial coordinates of trees, but also for the product of the heights (the mark in this case) of all pairs of individuals (Stoyan and Penttinen 2000). A value of $k_{m1m2}(r)$ close to 1 would indicate that the mark-pair products at a distance r depended on the spatial location of Smith fir individuals. In contrast, values of $k_{m1m2}(r) > 1$ or $k_{m1m2}(r) < 1$ indicated mutual stimulation (excess of mark pair products beyond a value explicable just in terms of locations of individuals) or inhibition, respectively. For instance, low values of the $k_{m1m2}(r)$ function at short distances would indicate that individuals belonging to pattern 2 (i.e., seedlings, juveniles) were shorter than expected if the points were located that distance apart from points of pattern 1 (i.e., juveniles, adults). The null model was built by fixing the marks of the pattern 1 while randomizing the marks of pattern 2 (Wiegand and Moloney 2014). We analyzed three bivariate patterns (adults *vs*. juveniles, adults *vs*. seedlings, juveniles *vs*. seedlings) of the mark tree height in both study plots (see also the bivariate patterns with two quantitative in Appendix S2).

Codispersion analysis

We used codispersion analysis to detect anisotropy in the present day bivariate height relationships among adults, juveniles and seedlings (Cuevas et al. 2013, Buckley et al. 2016a) using the mean height of each life stage in 10 × 10-m grid cells. This method uses a kernel function, in this case with a 10 m bandwidth, to quantify spatial covariation across a range of directions and spatial lags up to 38 m (¼ of the plot width). The observed codispersion values were compared to those generated by a 'random labelling' null model that re-shuffled the heights of trees 199 times (Buckley et al. 2016b).

Relating regeneration to climate

The climatic records in the study area, which were available from the 1960s onwards, were too short to evaluate linkages between treeline dynamics and directly measured climatic variables. Thus, we used two seasonal temperature reconstructions based on independent dendrochronological proxies to quantify climate-regeneration associations at multi-century scales (Liang et al. 2011). The first series was a summer mean minimum temperature reconstruction based on a tree ring-width chronology of Balfour spruce (*Picea likiangensis* var. *balfouriana* (Rehd. et Wils.) Hillier ex Slavin) growing in the southeastern Tibetan Plateau (Zhu et al. 2011). This reconstruction revealed an intense warming trend since the 1800s. A previous, related study on Smith fir (Liang et al. 2011) indicated that radial and longitudinal growth rates of this species were controlled by summer minimum temperature, and thus we expect that this will be the case in the present study. The second series was a cool-season mean temperature reconstruction (September until April) based on Qilian junipers (*Juniperus przewalskii* Kom.) from Wulan (Zhu et al. 2008), located ≈ 400 km NE from the study area. This second reconstruction was well-correlated with more recent

seasonal temperatures measured at our Nyingchi weather station ($r = 0.64$, $P < 0.001$) (Liang et al. 2011). It also showed a prominent rise in reconstructed cool-season temperatures during the 20th century. Here, we predict that cool-season temperatures will limit the survival of tree recruits at treelines, as shown previously (Kullman 2007, Renard et al. 2016).

We correlated the age structure data of Smith fir treeline trees with the reconstructed summer mean minimum and cool-season temperatures from 1760-2000. Since recruitment data were reconstructed and treelines may respond slowly to temperature changes (Camarero and Gutiérrez 2004), temperatures were averaged at 10-, 20-, 30- and 40-year intervals from 1760-2000.

We use the reconstructed age structure of living trees to infer variations in recruitment over time (Camarero and Gutiérrez 2004, Auger and Payette, 2010) assuming constant mortality rates (Wang et al. 2006, Liang et al. 2011). This assumption is supported by the following observations. First, the numbers of individuals of all stages (seedlings, juveniles, and adults) have increased over time in our reconstruction, indicating higher recruitment than mortality rates (Appendix S4: Figure S5). Whereas seedlings are typically the stage most susceptible to mortality (e.g., > 90%; Germino et al. 2002), in this study "seedlings" are well-established recruits between 3 and 30 years old. Given this fact, as well as the increase in older-stage individuals in these plots over recent time periods, mortality rates must clearly be relatively low and not increasing over the reconstruction time period, even with increased warming. Second, trees used in our population reconstructions are well within the 400-year lifespan of Smith fir and, aside from possible catastrophic events that may have caused episodic mortality over the past 200 years (which has not been recorded in local tree-ring chronologies – Liang et al. 2011), the older trees within our study plots should be reflective of the survival

rates at the earliest time periods in our study. To further support this, across both sampled plots we found only six dead adult trees (dbh = 17-62 cm; height = 4-14 m), which accounted for only 3.4% of the total sampled adults, suggesting a relatively low rate of adult tree mortality. Third, treeline position of Smith fir has remained stable over the past 200 years (Liang et al. 2011), including in relatively cold periods. Thus, there is no evidence along this line of inquiry to indicate significant mortality events. Finally, treeline densification inferred from our age-structure analysis is consistent with results from repeat landscape photography at treelines in Europe, American, and Asia (Camarero and Gutierréz 2004, Zier and Baker 2006, Devi et al. 2008), as well as at treelines in the Henduan Mountains of southeastern Tibetan Plateau located near our study region (Baker and Moseley 2007). Thus, it appears reasonable to use the reconstructed age structure at these plots to investigate changes in tree recruitment through time.

Data and code availability

All data and accompanying R code for the codispersion analyses are available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data-archive), dataset HF265.

RESULTS

Spatiotemporal patterns of tree age classes

Seedlings and juveniles were abundant in both study sites, and formed dense patches at treeline (Fig. 1; Appendix S4: Fig. S3). Intermediate-diameter classes ($35 \leq DBH \leq 40$ cm) included relatively few individuals (Appendix S4: Fig. S3). The distribution of age classes corresponded to recently expanding Smith fir treeline populations. Trees that had recruited

into the population within the past 5-50 years accounted for 84% (N1) and 89% (N2) of individuals (Appendix S4: Fig. S3). The reconstruction of the spatial patterns also revealed increasing tree density in both plots (Fig. 1). The most recent period (1982−2011 / 2013) contained the largest number of trees (Fig. 1e; Appendix S3: Table S1). The second largest recruitment peak occurred in 1952−1981 (Fig. 1d).

Adults, juveniles, and seedlings were randomly distributed within the treeline ecotone prior to 1921 (Fig. 1a and 1b), but seedlings from 1922-1951 were spatially clustered in the N1 site (Fig. 1c; Appendix S3: Table S1). Similarly, seedlings from 1952-1981 were spatially clustered at scales up to 6 to 8 m (Fig. 1d).

Adults and seedlings in the 1922−1951 cohort were spatially segregated (i.e., a significant negative spatial association) at distances of 1-5 m in the N1 site (Fig. 1c), whereas no spatial associations between adults and seedlings were found in the N2 site (Fig. 1c). During the 1952−1981 period, adults and seedlings were spatially segregated at 1-6 m scales (Fig. 1d). From the 1980s onwards seedlings were negatively associated with adults at 1-5 m scales (Fig. 1e).

No spatial associations were detected between adults and juveniles during the 1922−1951 period in both sites (Fig. 1c), but spatial segregation was found at 2-5 m for these two tree classes during the 1952−1981 and 1982−2011 periods (Fig. 1d, e). No significant spatial associations between adults and juveniles were detected in the N2 site (Fig. 1a-e).

No spatial associations were detected between juveniles and seedlings prior to 1951 in either of the study sites (Fig. 1 a-c). However, during the 1952-1981 period, aggregations of juveniles and seedlings were detected at scales of 1-4 m in the N2 site (Fig. 1d). From the

1980s onwards, a significant spatial aggregation was detected between juveniles and seedlings at 1-8 m (Fig. 1e).

In sum, spatial segregation was detected between adults and juveniles or seedlings since the 1950s, when Smith fir regeneration also was increasing in density. This spatial segregation intensified since the 1980s when regeneration accelerated, whereas spatial aggregation between juveniles and seedlings also increased recently (Appendix S3: Table S1).

Bivariate mark-correlation functions of tree height and recruitment

Juvenile trees were shorter than expected when they were located 1-3 m from adults in the N1 site and 1-4 m from adults in the N2 site (Fig. 2). On average, seedlings also were shorter than expected when located < 1 m from adults in the N1 site and 1-3m in the N2 site. Seedlings located 1-3 m from juveniles had larger height values than expected in the N2 site.

At 15 m from each target tree, height of adults and juveniles showed both segregation and aggregation with respect to the density of individuals recruited during the last 30 years (Appendix S4: Fig. S4). Segregation was due to neighboring trees having different heights, whereas aggregation was due to the clustering of recruitment within 4-5 m of adult trees.

Examination of $k_{m1}(r)$ suggested that nearby trees were shorter than expected. The bivariate mark correlation function $k_{m1m2}(r)$ revealed spatial associations between height and recruitment patterns (Appendix S4: Fig. S4). The function $I_{m1m2}(r)$ indicated a negative correlation between height and recruitment density at smaller scales. Specifically, tall trees tended to have fewer neighbors within 4-5 m than did shorter trees. Tree height and the density of individuals recruited during the last 30 years were negatively associated in both sites (N1: r = - 0.248, P = 0.018, radius = 15 m; N2: r = - 0.173, P = 0.001, radius = 5 m),

although neither of these correlation coefficients were significant after correcting for the presence of spatial autocorrelation (*P* corrected = 0.199; N2: *P* corrected = 0.653).

Codispersion analyses

Heights of adults and juveniles in the N1 site, and also adults and seedlings locations, were negatively correlated at most spatial lags and directions, except for a positive correlation observed in large lags along the NW direction toward the treeline boundary (interpreted in Fig. 4 as a change in color in observed codispersion values moving from the bottom of the codispersion graph towards the upper left corner of the graph), possibly reflecting the situation that consistently shorter tree heights near the treeline might be more similar to the heights of juveniles and seedlings lower down in the forest, causing a change in codispersion from negative to positive at these larger lags (Fig. 4). These patterns were significantly different from expected under a null model where tree spatial positions were fixed but observed heights were randomly assigned, for most spatial lags and directions for adults and juveniles. However, these patterns were significant for adults and seedlings considering small spatial lags (< 20 m) moving towards the treeline. In contrast, the heights of adults and juveniles in the N2 site were not significantly correlated, and adults and seedlings were only weakly negatively related (Fig. 4). In both sites, juveniles and seedling heights were positively correlated at all spatial lags and directions, although this was not significant for most spatial lags and directions in the N1 site, and for lags greater than 15 m in most directions in the N2 site (Fig. 4).

Recruitment dynamics and climate

Age structures suggested an increase in tree density in recent decades (Fig. 3). In both sites, tree recruitment was positively and significantly related to summer and winter temperatures

at 10 to 40-year long scales (Appendix S3: Table S2). However, the highest correlations were found between tree recruitment data and averaged summer minimum temperatures at 30-year long intervals in the N1 site and at 20-year long intervals in the N2 site (Appendix S3: Table S2). Tree recruitment in plot N1 during the 1960s and 1970s increased by 84% and 121% in comparison with the previous decade. Similarly, tree recruitment in plot N2 in the 1960s and 1970s increased by 95% and 376% as compared to the previous decade. In comparison with the 1922−1951 period, recruitment in the 1952−1981 period increased by more than 5 and 2.5 times in the N1 and N2 sites, respectively. Since the 1980s, tree recruitment has continued to increase, but at lower rates than in previous decades.

DISCUSSION

Our results indicate that regional warming has promoted treeline encroachment and densification since the 1950s, coincident with a warming rate that is unprecedented in the last 1000 years (Liu et al. 2005). Under the reasonable assumption of no significant changes in adult tree mortality rate, rising tree density in our plots is most likely attributable to an increased rate of tree recruitment that has been associated with climatic warming. Our findings are in line with results from similar studies in Europe and North America (Camarero and Gutiérrez 2004, Elliott 2011) and previous findings in the southeastern Tibetan Plateau (Liang et al. 2011). Our finding that increased tree density was related to warming also is consistent with other studies that have found that tree regeneration and growth in alpine treelines are primarily constrained by low temperatures (Harsch et al. 2009, Körner 2012). Nevertheless, the temporal scale is important because long-term tree recruitment responded positively to 20- and 30-year averaged summer minimum temperatures, implying a relatively

slow response of recruitment to climatic warming in our study system. These findings point to the possibility that a lagged recruitment response to climate might be a common feature of other cold-limited treelines (Camarero and Gutiérrez 2004, Kullman 2007), although coarse resolution of recruitment data limited our ability to test for a lagged response. Other factors explaining this lag could be the wave-like recruitment observed at alpine treelines, which is often related to episodic masting (Körner 2012).

Competition among canopy trees is a key feature of dense forests (Oliver and Larson 1996), but the role of competition as a result of densification in structuring alpine treeline forests has not been studied extensively. Our results suggest that competition has been increasing at our study sites. First, both increasing tree density and significant spatial segregation between seedlings or juveniles and adults at small scales (1-5 m) have occurred since the 1950s (periods 1952-1981 and 1982-2011/2013). Liang et al. (2011) and Wang et al. (2012) found no evidence for major disturbances in our study region, and the coupling of densification and spatial segregation further suggests that increased competition between recruits and mature trees is occurring among trees growing along the studied Tibetan treelines.

Second, the intensity of spatial segregation between juveniles or seedlings and adults at small scales increased during 1982−2013 relative to 1952−1981, suggesting that warming-induced densification has increased small-scale competition. Further, the spatial patterns of Smith fir changed from clumped seedlings during the earliest periods (prior to 1950) towards randomly or regularly located juveniles or adults in the most recent periods (1952−1981, 1981−2013), implying that competition has become increasingly important in shaping the spatial distribution of these trees. An alternative explanation of this pattern could be that the post-1950s warming resulted in a relaxation of cold stress strengthening the

coupling of treelines with climate and thus making tree recruitment less reliant on neighborhood facilitation. Tree clumping prior to the 1950s could indicate an association between cold stress and facilitation of recruitment through seedling protection from sunlight, frost, or wind stress (Maher and Germino 2006). Nevertheless, if density continues to increase, competition likely will have a negative impact on growth and survival, shifting processes in these forests towards those more like closed-canopy ecosystems (Getzin et al. 2006).

The spatial segregation of seedlings away from adult trees and the observed clustering of seedlings also are suggestive of a positive feedback-induced facilitation, an interaction that is known to play an important role in driving recruitment at treelines (e.g., Maher and Germino 2006). Whereas competition could play a dominant role in shaping future treeline dynamics under warmer climatic conditions (Tingstad et al. 2015), facilitation may still be a relevant process explaining aggregated recruitment patterns. For instance, the spatial aggregation that we detected between juveniles and seedlings suggests that juveniles may create favorable sites for seedling establishment (Callaway 2007). In addition, the aggregated spatial patterns of seedlings may promote a more favorable microenvironment by enhancing snow retention, which increases recruit survival (Batllori et al. 2009). Such enhanced facilitative mechanisms suggest that frequent bottlenecks in seedling establishment at treelines can be alleviated partially (Holtmeier and Broll 2007).

Increasing recruitment and competition within the Smith fir treeline population over the past 60 years follows expectations of the stress-gradient hypothesis, i.e., an increase in competition as abiotic stress diminishes (Choler et al. 2001, Callaway 2007, Chu et al. 2008, He et al. 2013). Temperatures since the 1950s have been among the warmest decades during

the past 1000 years in the Tibetan Plateau (Liu et al. 2005, Zhu et al. 2008), and it is reasonable to assume that low-temperature stress has been alleviated at Tibetan treeline, especially in comparison to the Little Ice Age. Ultimately, however, increasing competition will induce self-thinning of treeline populations, further suppressing the growth of recruits and inhibiting new recruitment.

The development of denser treeline forests in the Tibetan Plateau to the point where competitive processes predominate has important implications for future interactions between climatic change and forest dynamics. Given that future temperatures in the Tibetan Plateau are projected to increase by 2.6-5.2 °C by 2100 (Chen et al. 2013), we conclude that competition will play a more important role in driving treeline dynamics than it has in the past. At some point, increasing competition between adults and juveniles or seedlings could counteract any positive effects of future warming on tree growth in these treeline forests. Additional sites and species should be scrutinized in a global comparison of alpine treelines to properly quantify the pattern and pace of their transitions towards more-dense subalpine forests. Nonetheless, our results suggest that increasing densification as a result of warming at alpine treeline ecotones in future years may promote a potential switch from facilitation to competition, particularly as more juveniles and seedlings transition to adults. To better understand how treelines may respond to future warming, further investigation into climate-driven switches between facilitation and competition over time and space (e.g., Renard et al. 2016) is warranted.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi//xxxxxxxx/suppinfo

Appendix S1. Field sampling.

Appendix S2. Point-pattern analyses.

Appendix S3. Statistical tables.

Appendix S4. Site map and additional figures.

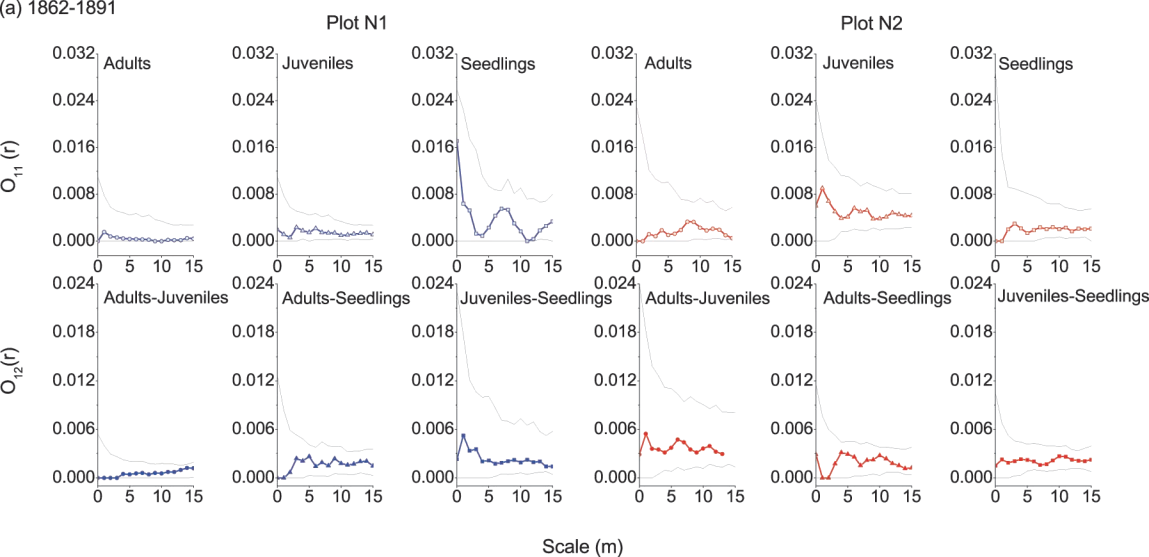
Figure legends

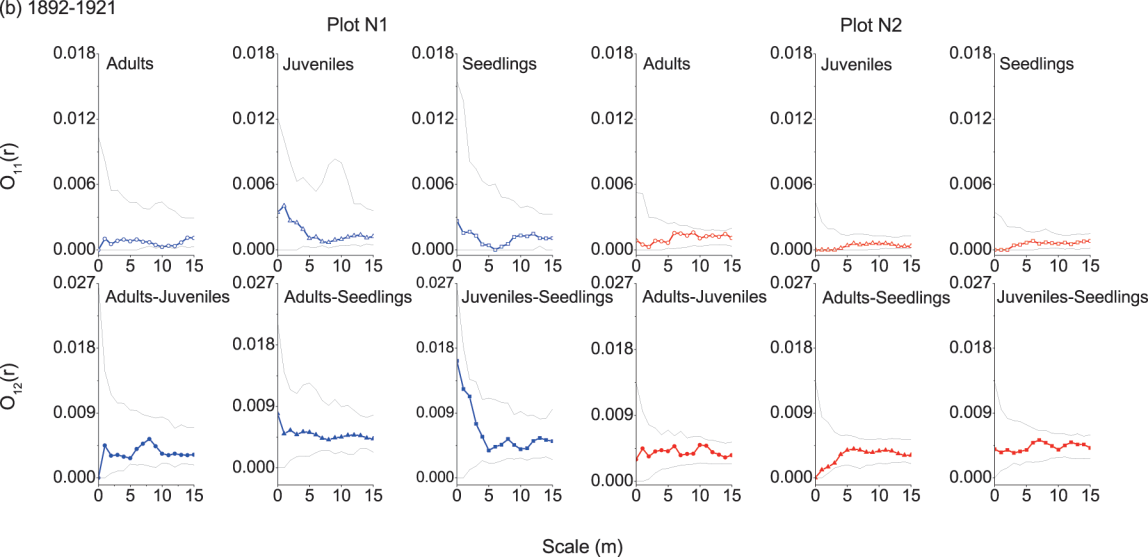
Figure 1. Univariate and bivariate spatial patterns and analyses obtained for the two Smith fir treeline sites. We considered three age classes of Smith fir individuals (adults, juveniles and seedlings). Spatial pattern analyses were conducted during the past 150 years over the following 30-year intervals: (a) 1862-1891, (b) 1892-1921, (c) 1922-1951, (d) 1952-1981 and (e) 1982-2011/2013. Figures in the first row correspond to the univariate ($O_{11}(r)$ statistic), whereas figures in the second row correspond to bivariate ($O_{12}(r)$ statistic) point pattern analyses, respectively. Colored lines with symbols indicate the $O_{11}(r)$ or $O_{12}(r)$ statistics, whereas black lines correspond to the upper and lower 99% bounds of the simulation envelopes. In the univariate case, values of the calculated statistic located above or below the upper and lower envelopes indicate significant aggregation or hyperdispersion (regularity), respectively. In the bivariate case, values of the calculated statistic located above or below the upper and lower envelopes indicate significant attraction or repulsion, respectively (see also Appendix S3: Table S1).

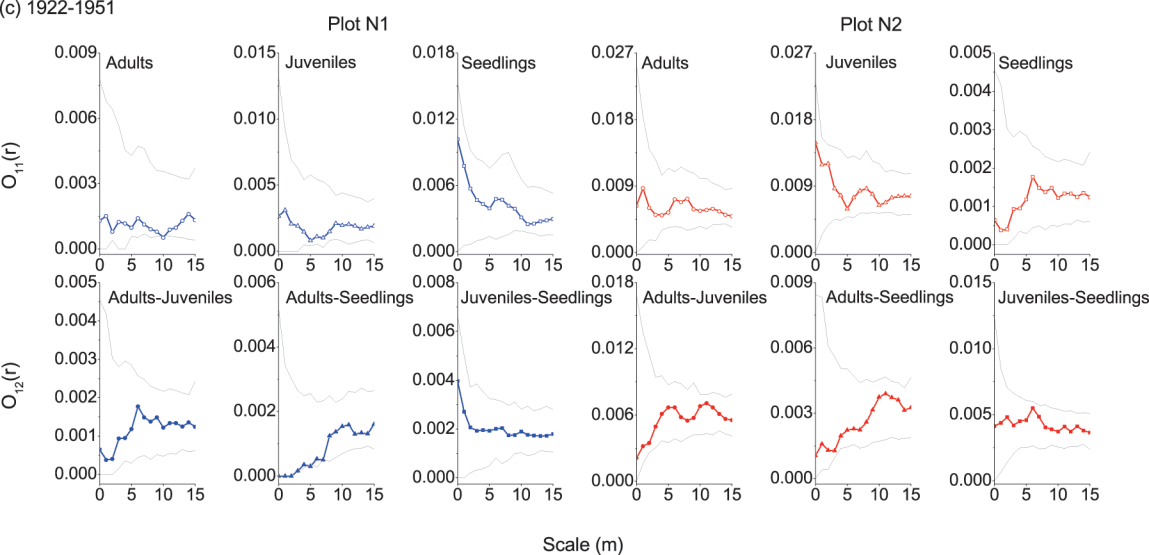
Figure 2. Mark correlation functions ($k_{m1m2}(r)$, upper figures) based on the spatial patterns of tree height in N1 (a) and N2 (b) treeline sites. The functions were calculated by relating the spatial locations of adults vs. juveniles, adults vs. juveniles or juveniles vs. seedlings. The continuous lines with symbols correspond to the calculated functions, whereas continuous and dashed lines show the null model and the 99% bounds of the simulation envelopes, respectively. The Goodness-of-Fit (GoF) tests and their significance levels (P) are also shown. Note that values of $k_{m1m2}(r)$ close to 1 indicate that the mark pair products at a distance r only depend on the spatial location of Smith fir individuals.

Figure 3. Variations in reconstructed summer mean minimum and winter half-year mean temperatures (a) and temporal dynamics of (log+1 transformed) Smith fir recruitment at decadal resolution (b) in the two treeline plots (white and gray bars correspond to N1 and N2 plots, respectively).

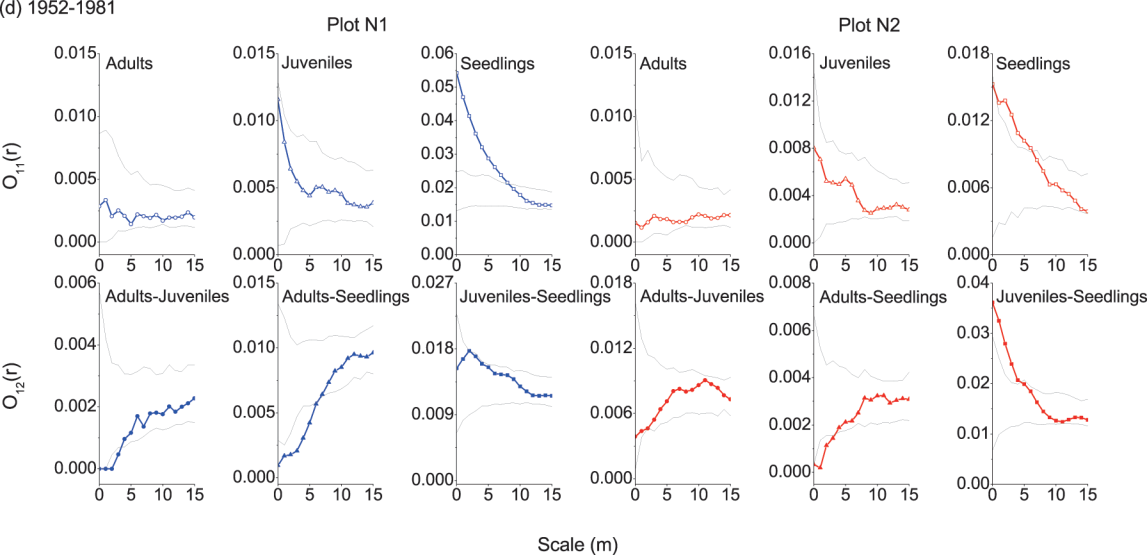
Figure 4. Recent bivariate point-pattern maps (far left panel) for adult trees (large, green points), juveniles (intermediate, orange points) and seedlings (small, black points) in the N1 (a-c) and N2 (d-f) treeline sites and their resultant codispersion analyses of height. Codispersion graphs show the observed codispersion values for associations between the heights of adults and juveniles (a and d), adults and seedlings (b and e) and juveniles and seedlings (c and f) for a range of spatial lags within each site (left; contour lines = 0.1), the observed values minus the values expected under a 'random labelling' null model (center), and the significance (red), or not (blue), at the $P < 0.05$ level. The random labelling model was used to calculate 199 expected codispersion values for randomly-assigned heights at the observed tree positions.

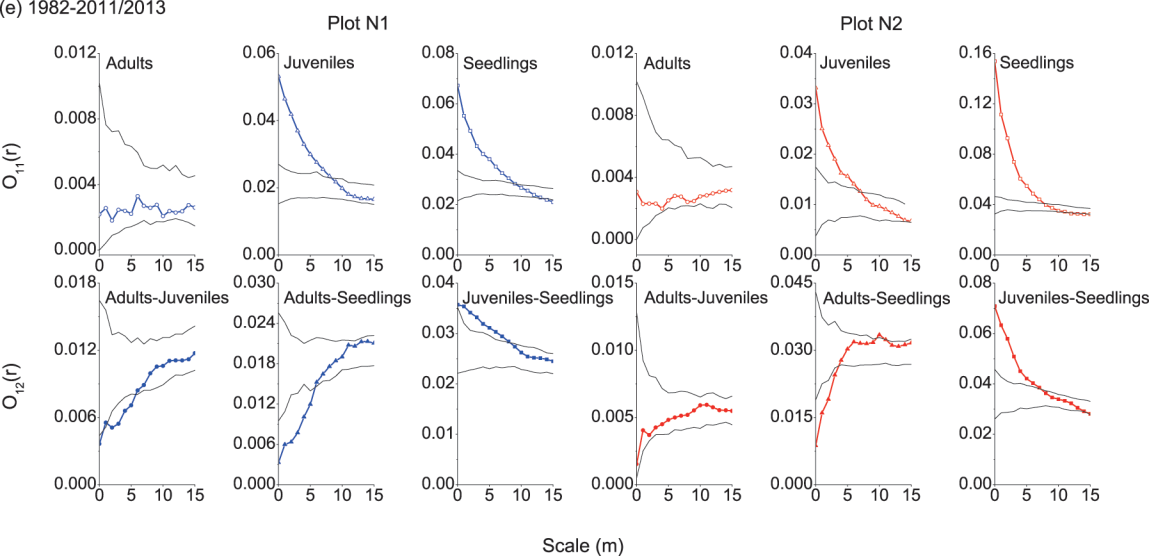

(a) 1862-1891
Plot N1
Plot N2
Adults
Juveniles
Seedlings
Adults
Juveniles
Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
O11 (r)
O12(r)
Scale (m)

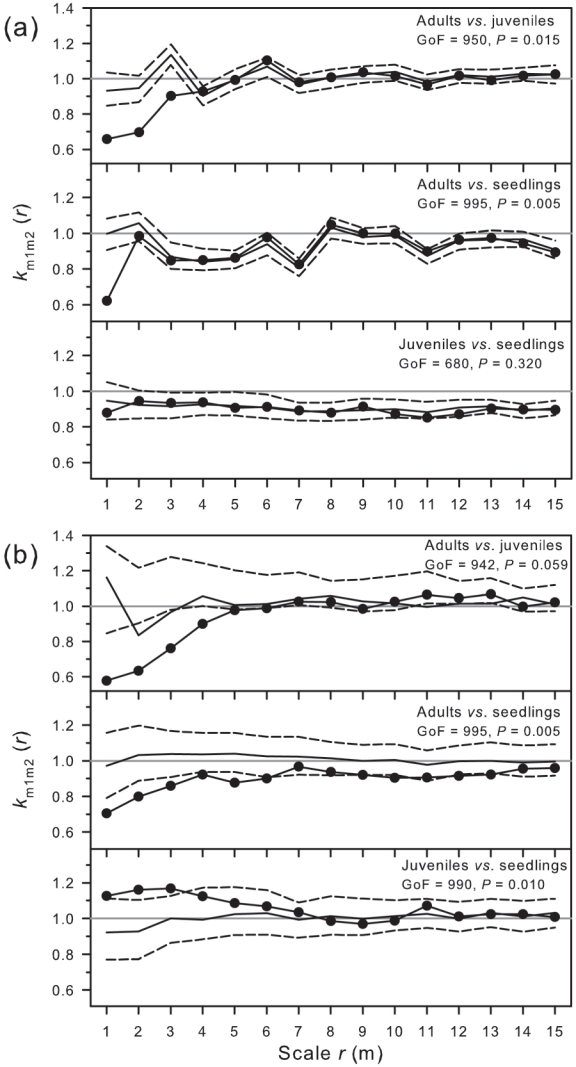

(b) 1892-1921
Plot N1
Plot N2
Adults
Juveniles
Seedlings
Adults
Juveniles
Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
O11(r)
O12(r)
Scale (m)

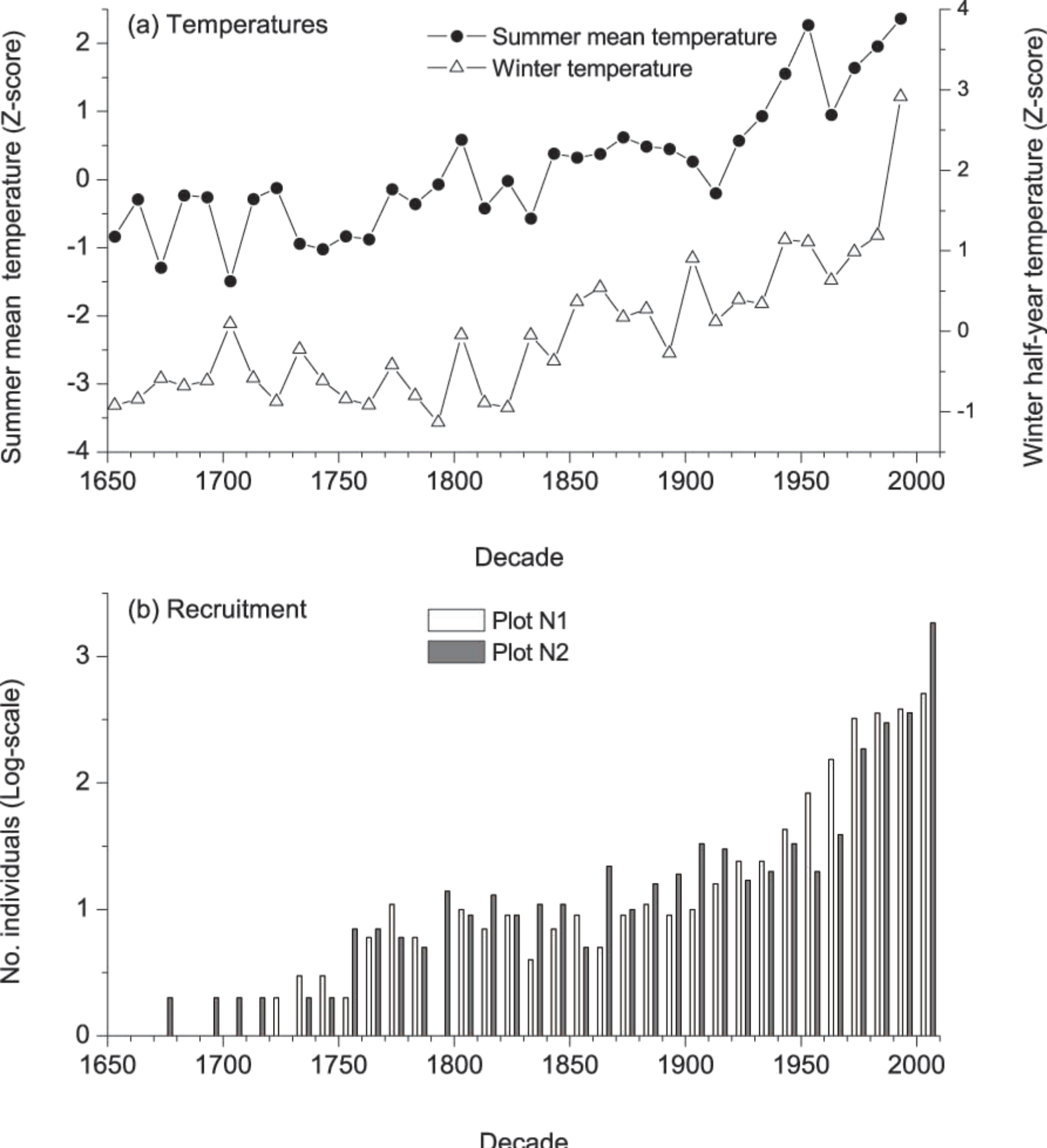

(c) 1922-1951
Plot N1
Plot N2
Adults
Juveniles
Seedlings
Adults
Juveniles
Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
O11(r)
O12(r)
Scale (m)

(d) 1952-1981


Plot N1
Plot N2
Adults
Juveniles
Seedlings
Adults
Juveniles
Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
O11(r)
O12(r)
Scale (m)


(e) 1982-2011/2013
Plot N1
Plot N2
Adults
Juveniles
Seedlings
Adults
Juveniles
Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
Adults-Juveniles
Adults-Seedlings
Juveniles-Seedlings
O11(r)
O12(r)
Scale (m)


(a)
Adults vs. juveniles
GoF = 950, P = 0.015
Adults vs. seedlings
GoF = 995, P = 0.005
Juveniles vs. seedlings
GoF = 680, P = 0.320
k m1m2 (r)
(b)
Adults vs. juveniles
GoF = 942, P = 0.059
Adults vs. seedlings
GoF = 995, P = 0.005
Juveniles vs. seedlings
GoF = 990, P = 0.010
k m1m2 (r)
Scale r (m)


(a) Temperatures
Summer mean temperature
Winter temperature
Summer mean temperature (Z-score)
Winter half-year temperature (Z-score)
Decade
(b) Recruitment
Plot N1
Plot N2
No. individuals (Log-scale)
Decade

Observed point pattern

Observed codispersion

Observed minus expected codispersion

Significance

(a)

(b)

(c)

(d)

(e)

(f)

Y (m)

Spatial lag in Y (m)

X (m)

Spatial lag in X (m)

1.0
0.5
0.0
-0.5
-1.0

0 50 100 150

10 20 30 40

-40 -20 0 20 40